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DECLINE IN THE FREQUENCY OF THE WHITE MORPH OF THE MONARCH BUTTERFLY (*DANAUS PLEXIPPUS PLEXIPPUS* L., NYMPHALIDAE) ON OAHU, HAWAII

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ABSTRACT. The frequency of a white morph of the monarch butterfly *Danaus plexippus plexippus* on Oahu, Hawaii was observed to increase from less than 1% in 1965 to approximately 8% in 1988–1989, and then to decrease in the nine year period from 1988–1989 to 1997–1998 to about 1.7%. The increase was attributed to the accidental release in 1965 and 1966 of two species of predatory birds, selective predation of these birds on the orange morph and the supposedly greater crypsis of the white morph. It is proposed that the decrease in the proportion of the white morph has been caused by a change in the predatory behavior of these birds, a switch from predation on adults to predation on larvae. The larvae of the two morphs are indistinguishable.

Keywords: *Danaus plexippus,* polymorphism, white morph.

There are many examples of balanced and transient polymorphism in Lepidoptera. In most cases, the polymorphism involves a difference in wing colors or pattern. Polymorphism has also been observed in the larvae and pupae of some species (Clarke et al. 1963, Smith et al. 1988). Although many of these polymorphisms are thought to be the result of Batesian or Müllerian mimicry (Ford, 1953, Smith et al. 1993), the most famous example of polymorphism in Lepidoptera, that in *Biston betularia,* involves cryptic coloration. The frequency of the melanic phenotype of these moths increased dramatically in England, Netherlands, and the U.S. (Clarke et al. 1985, Brakefield 1990, Grant et al. 1996), but has declined since the 1950's. In Manchester, the melanic morph increased from 0% to 98% in 100 years (Kettlewell 1973); in Merseyside the melanic form decreased by 50% as pollution decreased and tree surfaces became lighter (Clarke et al. 1985). Polymorphism has also been observed in the butterfly *Danaus chrysippus* L. (Smith et al. 1993). Among four forms of *D. chrysippus* in Kampala, Uganda, the form *alcippus* increased from 16% to 71% and the form *aegyptius* decreased from 66% to 24% in approximately 80 years Hybridization, Batesian mimicry and Müllerian mimicry are thought to be involved in the origin of this polymorphism. The changes in frequency are thought to be due to recent habitat alteration; allopatric populations previously isolated by forest barriers are now hybridizing. Both these examples involved rapid change in morph frequency.

The monarch butterfly, *Danaus plexippus*, which appeared in Hawaii in the mid 1800's (Zimmerman 1958), is dimorphic for wing color on Oahu, Hawaii. In addition to the normal orange morph, there is a white morph which has white scales in place of orange on all wings (Riotte & Uchida 1978). The pattern of black scales is the same in both morphs. Genetic crosses have shown that the white morph is homozygous for an autosomal recessive allele (Stimson & Meyers 1984).

The history of the white monarch in Hawaii goes back to the 1890's. A white monarch from Hawaii was received in the mid 1890's by the Walter Rothschild collection (now in the Natural History Museum, London: Vane-Wright 1986). In Zimmerman's (1958) monograph of Hawaiian insects, there was no mention of a white morph in Hawaii, but in a collection of 600 monarch pupae made on Oahu by Mitchell (1966) in 1965, a small percentage, less than 1% of eclosing adults, were white individuals. In the early 1970's, the frequency of the white morph increased and reached approximately 5% by the mid 1980's (Stimson & Berman 1990).

Both morphs of the butterfly oviposit, feed and bask on the same host plant, the introduced milkweed *Calotropis gigantea*. These plants have large white inflorescences, and their leaves have a white pubescence, particularly on the underside. Stands of these plants occur in residential areas and attract large numbers of butterflies from November to February or March. When the butterflies are common at these stands, the introduced, insect-eating, red-whiskered bulbul (*Pycnonotus jacosus*) and red-vented bulbul (*Pycnonotus cafer)* can be seen searching inside the canopy for larvae and flying off with them to neighboring trees (pers. obs.).

Stimson and Berman (1990) suggested that the reason for the increase in frequency of the white morph

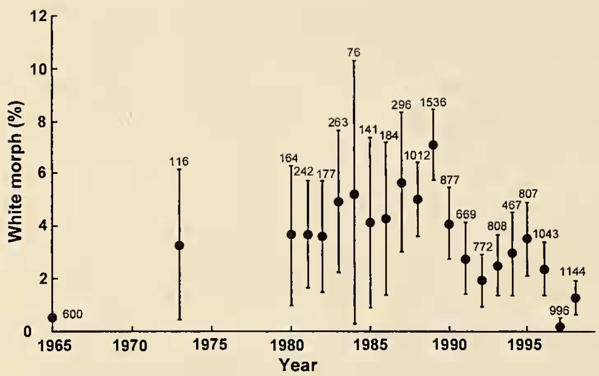

FIG 1. Proportion of white monarch adults emerging from pupae collected on the campus of the Univ. of Hawaii, Manoa, Oahu. The figure for 1965 is for a collection of 600 pupae made by Mitchell (1966). Vertical bars are 95% binomial confidence intervals for the proportions. The period of peak monarch abundance occurs in the winter spring and straddles the change in year; the annual proportion of whites has been plotted at the year of the spring of the peak. Values in association with each point are the numbers of monarch which eclosed and were scored each year.

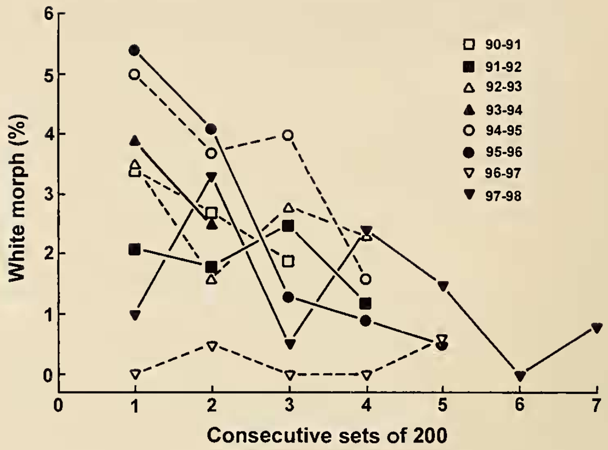

FIG. 2. Decrease in the proportion of white morph through each season during the years of decline of the proportion of the white morph in the University of Hawaii population on Oahu. All points are based on a minimum of 200 butterflies.

was predation by these birds. These birds escaped from captivity on Oahu in 1965 and 1966 (Williams 1983) and have spread to most areas of Oahu (Williams & Giddings 1984, R. Pyle, Bishop Musuem, pers. comm). Red-vented bulbuls occur at most lower elevations (<200 m) of Oahu. Red-whiskered bulbuls have a more restricted distribution and are more common in higher elevations and in the central parts of Oahu (Williams & Giddings 1984). The abundance of these two species of birds has increased about a thousand fold in Honolulu between the mid 1960's and the early 1980's according to the Audubon Christmas censuses (Williams & Giddings 1984). These birds are not deterred by the cardiac glycosides in the monarch's tissues and are documented to feed on monarch larvae and adults (Stimson & Berman 1990). The date of escape of these birds and the subsequent rise in frequency of the white morph coincide.

The white morphs were thought to be more cryptic than the orange form when associated with the milkweeds, because their white wings do not contrast with the whiteness of the inflorescences and the whiteness of the leaves caused by pubesence. Because of this presumed crypsis, it was proposed that white morphs had a lower risk of predation (Stimson & Berman 1990). The decrease in the proportion of white individuals since the 1988–1989 season requires a reexamination of this hypothesis. This study examines the change in frequency of white *D. plexippus* at one collection site on Oahu for the last 25 years and offers a possible explanation for the increase and decrease in frequency of the white morph.

MATERIAL AND METHODS

The frequency of the two morphs was determined at eclosion by collecting pupae from the field and scoring adults daily as they emerged in captivity. Pupae were collected from two stands of milkweed, *Calotropis gigantea*, at Edmondson Hall on the University of Hawaii campus, Honolulu, Oahu, Hawaii. The two stands are 60 meters apart on opposite sides of a building. Each stand consisted of 9 plants and each plant was approximately 1–2 m in diameter and 3 m tall. Other stands of plants occur on campus and in nearby residential neighborhoods. After the sex and morph of each adult was determined, the individuals were released. Since the 1987–1988 season, searches have been exhaustive, thus the numbers of adults in each morph are almost a complete collection of pupae produced at the Edmondson stands.

Bulbuls were observed to prey on larvae and adults at the stands of milkweed. After capturing adults the birds frequently took the prey to the ground, broke off their wings, and then flew off with the body. Birds were not seen consuming the bodies. During each of our searches for pupae, a search was also made for wings lying on the ground near the bushes.

RESULTS

Adult monarch butterflies are present the year-around on Oahu, but the peak of the breeding lasts for only 2–3 months, generally between December and February. During this period, individual milkweed plants can have hundreds of eggs and larvae, and in some years the bushes are stripped of leaves. As many as ten adults can be seen at any time at each of the two milkweed stands during the peak of abundance.

The proportion of white adults which emerged from pupae collected at each of the Edmondson stands increased during the 1970's and 1980's, and reached a peak of 7.3% in the 1988–1989 season (Fig 1). Since that season, there has in general been a decrease in the proportion of white individuals. In the latest season (1997–1998), only 1.7% of the collection were white individuals. A polynomial regression (binomial) was fitted to the data from 1980 on, i.e., when the sampling intervals were constant, 1 year apart. This regression shows that fitting the polynomial results in a significant reduction in unexplained sums of squares ($F = 12.85$, df = 2,19, $p < 0.0004$), and that there is a significant quadratic term. The signs of the terms of the polynomial indicate that the shape of the fitted curve is a hyperbola

$$(Y = -0.945 + 0.024X - 0.0001X^2).$$

To test whether the proportion of the white morph changed within each annual monarch season, the record of daily emergences within a peak season was divided in half, the first 50% of emergences, second 50% of emergences, and the proportion of white individuals in each half of the collection was calculated. Only peak seasons with collections of 200 or more pupae were used in this analysis. The proportion of the white morph was significantly higher in emergences from the first half of the peak season by a non-parametric Wilcoxon's sign rank test (16 peak seasons, $p < 0.05$). The proportion of white morph over the course of each season was also computed by dividing each season's emergences into consecutive groups of 200 emergences, and then calculating the proportion of white morph in each of these consecutive groups. The proportions calculated in each season were then plotted against date; the proportion of white individuals starts relatively high at the beginning of most seasons and then declines as the season progresses (Fig. 2).

During the 1980's, bulbuls could frequently be seen attacking flying adults. Many wings could be collected from the ground near or under the milkweed bushes during the annual peak season of monarch abundance. Since 1989–1990 season, fewer wings have been found (less than 10 per season), fewer attack on adult monarchs have been seen and bulbuls have been seen to prey more heavily on larvae than on adults. All these observations suggest that there is less opportunity for differential mortality of adults as a result of predation.

DISCUSSION

The proportion of white monarchs increased from 1966 to 1988–1989 and then decreased in the last nine years. An explanation for the increase in the proportion of white individuals, proposed in Stimson and Berman (1990), was that the white butterflies are less conspicuous against the whitishness of the pubesence of the leaves and the white of the flowers of *Calotropis gigangtea*, particularly when large numbers of butterflies frequented the milkweeds. As a result of this reduced conspicuousness if was proposed that the white individuals had a higher fitness than orange individuals. In support of this hypothesis is the fact that the increase in the proportion of white individuals in Honolulu appears to coincide with the date of escape of the two alien bulbul species on Oahu in 1965 and 1966 (Williams 1983). Following their escape these birds increased rapidly in the Honolulu area (Williams & Giddings 1984), and in the subsequent 15 years have spread into all the low elevation sites on Oahu where milkweeds are common (R. Pyle, Bishop Museum, pers. comm.). In the previous approximately 100 year history of the monarch in Hawaii the white individuals were evidently never very common. The differential predation exerted by these birds during the 1980's was detectable in the collections of wings; a higher proportion of orange wings were found in collections made from the ground around the bushes than the proportion of orange butterflies in the contemporaneous flying population (Stimson & Berman 1990). The role of these birds in causing the increase in frequency of the white morph is also supported by the fact that in collections of at least 100 butterflies made on Maui, Hawaii and Kauai in the late 1980's, the peak of abundance of the white morph on Oahu, no white butterflies were found. The lack of white individuals on these islands is consistent with the fact that bulbuls have not yet established breeding populations on islands other than Oahu, and thus the selective pressure for the increase in whites has not existed on these other islands.

The decline in the proportion of white individuals since 1988–1989 may be the result of a change in the predatory behavior of bulbuls. This change is evident in the decrease in the number of wings of either color collected at the milkweed bushes since the beginning of the decline; over 100 wings could be collected from the ground beneath and around the milkweed stands at Edmondson Hall during a monarch season (Stimson & Berman 1990). Now, very few wings are collected during a season. The bulbuls now seem to prey more heavily on larvae than on adults, especially at the peak of abundance. Because we cannot distinguish which larvae will turn into white or orange adults, we assume that there is no differential predation on larvae which will turn into white or orange individuals. With this proposed shift to predation on larvae, white adults are presumably no longer at a selective advantage. Selection coefficients have not been calculated for the periods of increase and decrease in the frequency of the white morph because: there are many generations of this butterfly per year, generations overlap, abundances differ greatly among generations, and because there is evidence (Fig. 2) that during the decline of the white morph since 1989, the direction of selection is reversed within the course of a year. Since 1988–1989, the proportion of the white morph has tended to be higher at the start of each season than at the end of the last season. Unfortunately no data is available to directly test the idea that a switch in predation behavior, a switch from preying primarily on adults to preying primarily on larvae, took place in the late 1980's.

While white individuals seem to have been at a disadvantage in the last 9 years, they have not disappeared from this population. The fact that white individuals constitute a higher proportion at the beginning of the annual peak of abundance (Fig. 2) suggests they may be at a selective advantage outside the period of peak abundance. When monarchs are at lower density, larval monarchs may not be a conspicuous resource drawing predators to the milkweeds. At such times, the adults may be the more conspicuous resource, and among the adults the white individuals may be less conspicuous than the orange, giving rise to an increase in the proportion of white adults in the non-peak part of the year. When the density of larvae and adults becomes very high, hunting and predation become very concentrated at the residential stands of milkweeds because of the conspicuousness of the resource. Several bulbuls can be feeding at a stand of milkweeds and sometimes both species of bulbuls are in the area of the milkweed stands. At such times mortality caused by predation evidently falls most heavily on larvae, and therefore indiscriminately with regard to the color of the adults. The proportion of white individuals in the population possibly declines during the peak season because white butterflies are at a disadvantage due to some process such as mate selection. Since the white morph seems to enjoy a selective advantage outside the peak season, this polymorphism could persist for some time.

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